On the behaviour and social organisation of Agile wallabies, *Macropus agilis* (Gould, 1842) in two habitats of northern Australia

By W. Dressen

Lehrstuhl für Verhaltensphysiologie, Fakultät für Biologie, Universität Bielefeld, Germany

Abstract

The behaviour, population characteristics and patterns of association of the agile wallaby *Macropus agilis* were recorded over five months during the dry and late dry season in two habitats at Kapalga, Northern Territory, Australia. Mean population density of wallabies in a monsoon forest was estimated to be approximately 6.5 times greater than in open eucalypt woodland. In both populations, the sex ratio of adult animals was significantly biased towards females. The mean size of associations was higher in the monsoon forest. Larger associations in both habitats were temporary and represented aggregations at spatially concentrated resources: foraging areas, water and shelter sites. Females with their independent offspring and small males were essentially solitary. Large and medium-sized males were always seen associated with females of different size classes. Gregariousness in *M. agilis* was correlated with population density which appeared to depend on the habitat and the distribution and availability of food. The solitariness of young males and stability of female groups in the eucalypt woodland may be a result of females remaining within the home range of their mothers whereas young males may separate and disperse soon after weaning.

Introduction

The sandy or agile wallaby *Macropus agilis* (Gould, 1842) is the most common macropodid of the northern tropical region of Australia inhabiting open savanna woodland as well as more dense riverine and monsoon forests with adjacent grasslands (BOLTON 1974; MERCHANT 1983). Like other larger macropodids, the species is dimorphic, and males reach sizes between 20–30 kg, about double the size of females (MERCHANT 1983; NEWSOME 1983). In spite of its abundance, surprisingly little is known about its social organisation and ecology. JOHNSON (1980) analysed group composition of *M. agilis* in North Queensland not knowing identities of individuals. He found single animals as the most commonly observed social unit and suggested that "in the small groups the most frequent relationship appeared to be the sexual assocation between female and male; in the larger groups feeding seemed to be the basis of association ...". In his socio-ecological study on three sympatric macropodid species in the Northern Territory, CROFT (1987) likewise concluded that *M. agilis* is essentially solitary.

This study presents results of a five months investigation on two populations of agile wallabies in the wet-dry tropics of Northern Australia. Here, the availability of resources fluctuates greatly each year, resources become limited and clumped in the late dry season, and abundant but spread out during and following the wet season (RIDPATH 1985). The study was conducted during the dry and late dry season in two habitats with obvious differences in the availability of water and food. The objective of the study was to describe the behaviour of individuals and of associations, and to compare the population characteristics at both sites. Furthermore, the analysis of the composition and stability of

Identifying individuals

Many individuals could be identified on the basis of the shape, number and location of ear notches and black spots on the ears. However these markings could only be reliably recognised at distances up to 80 m using a 10×40 binoculars. Mature females were easily recognized by natural ear markings. Other individual external features included a missing tonus of the tail (during hopping), a blind/missing eye, and distinctive face scars. Individual variations in the colour of the fur were less conspicuous. The white facial stripe – as used for individual recognition in the whiptail wallaby, *Macropus parryi* (KAUFMANN 1974) – was not a useful distinguishing feature in *M. agilis* because of its uniform shape. In total 16 male and 28 female wallabies could be identified using external features.

Definitions of groupings

Two individuals were assumed to be associating when within about 50 m of each other. A group was defined as an association of individuals resting and moving close together with attentiveness for and orientation to the behaviour of the other group member(s) resulting in coordinated movement patterns. The lability of an association was defined as the number of wallabies joining or leaving a grouping during a 30 min observation bout divided by the number of animals at the beginning of the observation bout (JOHNSON 1989b). Average values of this lability index ("group flux") were calculated for five size/sex classes of single and associated foraging animals (single; female with young-at-foot; single sex association N = 2, and N $\geq$ 3; mixed sex association N = 2, and N $\geq$ 3).

Results

Habitat utilization

In the monsoon forest wallabies rested during daylight hours between buttresses of large trees, in shallow depressions which they scraped or beneath fallen logs and dense vegetation. Wallabies were active during mornings and afternoons when they moved between 0.6 and 1.5 km (N = 12) from their resting sites. They dispersed within the forest digging for roots and foraging for fallen fruits mainly *Ficus racemosa, Carpenteria* sp. and flowers and green fruits of the Kapoktree (*Bombax ceiba*). Between 19.30 and 21.00 h between 2 and 12 wallabies (mean: 5.3, N = 12 counts) were seen grazing on the grassy floodplains adjacent to the monsoon forest. When spotlighted they immediately escaped to the forest.

In July and August (dry season) wallabies in the eucalypt woodland grazed close to billabongs only during the night and moved daily to the billabong from non-adjacent areas (> 0.5 km). From September to October (late dry season) wallabies shifted their main activity centres closer to the billabong. They were observed drinking and grazing on the open areas close to the remaining water during morning and late afternoon hours (Fig. 1). They spent the hottest part of the day in the adjacent woodland resting usually under tussocks of grass.

Patterns of activity

During the day wallabies in the monsoon forest site were more active, especially in foraging, than wallabies in the eucalypt woodland (Fig. 1), and they rested predominantly between 12.00 and 15.00 h compared to 11.00–17.00 h for the eucalypt woodland population. Activity bouts for the eucalypt woodland wallabies were from 7.00–10.00 h and from 16.00 h on. During these periods most wallabies drank once every day, others were observed drinking every second day. As the dry season progressed, the water level of the billabong rapidly receded. This provided the major source of green grasses and forbs for wallabies in both day and night feeding sessions. After arriving at the billabong wallabies spent 4.1 $\pm$ 2.4 min (N = 48) drinking followed by 38 $\pm$ 14.6 min (N = 48) grazing close to the water. When grazing on this open area, wallabies spent more time exhibiting alert behaviour than wallabies which foraged in the monsoon forest.

(a)

(b)
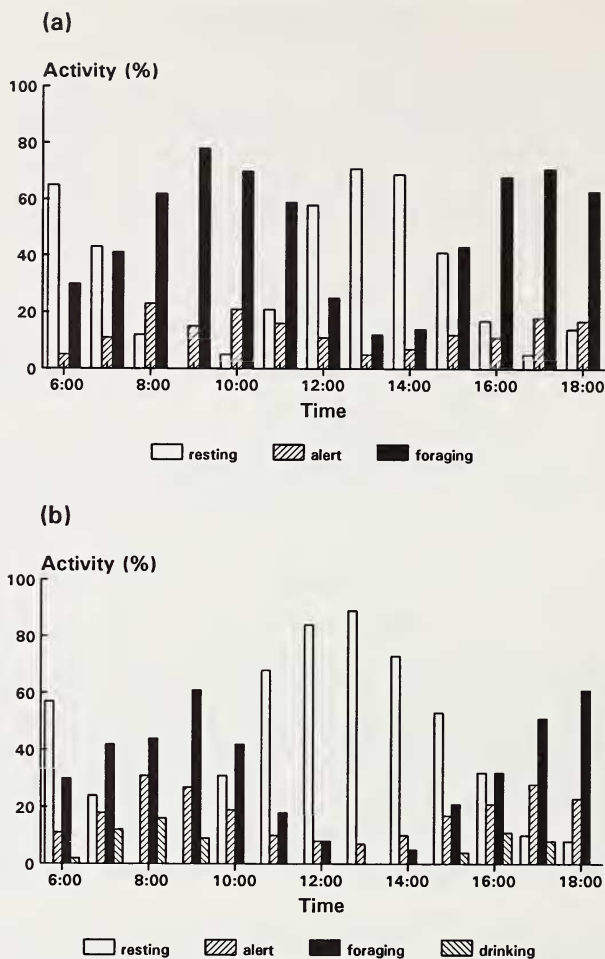
Fig. 1. Activity budget of *Macropus agilis* in monsoon forest (a) and in eucalypt woodland (b)

Density and sex ratio

Table 1 shows the mean density of wallabies calculated for both habitats from 24 transect counts. If both seasons and transect lines per habitat are combined the mean density at the monsoon forest population was approximetely 6.5 times larger than the eucalypt woodland population. The increase in density in the woodland between early and late dry season was probably due to wallabies congregating on areas with permanent water. The density in the monsoon forest remained stable throughout. Density was lower at line 2 placed in the transition zone adjacent to the eucalypt woodland.

At both study sites the overall sex ratio (male : female) was significantly biased towards females. In the open woodland sex ratio was 0.535 (N = 109, χ^2 = 9.99, P < 0.01), in the monsoon forest sex ratio was 0.57 (N = 168, χ^2 = 12.59, P < 0.01). Sex ratio disparity was most pronounced in medium and large size classes, whereas sex ratio in the small size class was not significantly different from 1.0 (Tab. 2). These data suggest that there was a trend of bias of sex ratio towards females with increasing age.

Table 1. **Mean densities ($\pm$ SD) of *Macropus agilis* (km^{-2}) observed during dry and late dry season in two habitats**

Habitat		Dry season		Late dry season	
Eucalypt	line 1	7.12	$\pm$ 5.74	16.67	$\pm$ 9.23
woodland	line 2	2.78	$\pm$ 3.28	1.67	$\pm$ 2.89
Monsoon	line 1	61.67	$\pm$19.08	58.33	$\pm$25.76
forest	line 2	31.6	$\pm$16.75	30.83	$\pm$17.54

Table 2. **Sex ratio (male : female) of *Macropus agilis* in two habitats**

Habitat	Size class	Males	Females	Sex ratio	χ^2	P
Eucalypt	large	8	22	0.364	6.53	<0.01
woodland	medium	19	43	0.442	9.29	<0.01
	small	11	6	1.833	1.47	>0.225
Monsoon	large	15	50	0.30	18.85	<0.001
forest	medium	19	35	0.543	4.74	<0.05
	small	27	22	1.227	0.51	>0.475

P: significance of difference from a 1:1 ratio (χ^2-Test).

Social behaviour

Agile wallabies interacted with conspecifics at a rate of 0.85 interactions per hour (N = 91.5 hours of observation of associated wallabies excluding consort interactions). There were 44 (56.4 %) agonistic, and 26 (33.3 %) sexual and 8 (10.3 %) other non-agonistic interactions.

The most frequent agonistic interaction (0.37 h^{-1}) was the approach-retreat-encounter (N = 34; 43.6 %): one animal approached a conspecific which retreated after short mutual sniffing (N = 14; 17.9 %) or without a sniffing contact (N = 20; 25.6 %). Members of all age/sex classes could be involved in this type of agonistic interaction. Those sequences preceded by a naso-nasal or naso-body contact often involved biting, grabbing and/or kicking by one animal whereas the other usually crouched and jumped away.

The most distinctive agonistic behaviour was standing on tip-toes with a crouched body posture using the tail as a prop (Fig. 2). The body position resembles that of the "stiff-legged walk" described for other macropodids (cf. KAUFMANN 1974; COULSON 1989) except that the opponents did not walk but stood motionless for several seconds in frontal or broadside position with their head lowered. This behaviour was shown in agonistic encounters between and within both sexes. It was performed by either or both interacting animals and resulted in the retreat of one animal (N = 6) or exaggerated grooming followed by grazing of both opponents (N = 2). Fights were rarely seen (N = 2) and were characterized by grappling and sparring between both opponents. Both fights were performed by Ms-males with no obvious winner. Stereotyped agonistic displays described for large macropodids (cf. GANSLOSSER 1989) were not seen in the field. In captivity, grass-pulling combined with standing-high and rubbing of grass and branches against the chest has been observed in male agile wallabies following agonistic encounters.

Observations of anoestrous sexual interactions (N = 26; 33.3 %; 0.28 h^{-1}) were similar to that of other macropodids: while the male pawed a female's tail he had a partly or fully erected penis and simultaneously lashed his tail, and nosed the female's cloaca. This "sexual checking" (KAUFMANN 1974) usually caused the female to retreat but occasionally elicited urination. Nosing of the cloaca was also observed twice between males. In both encounters
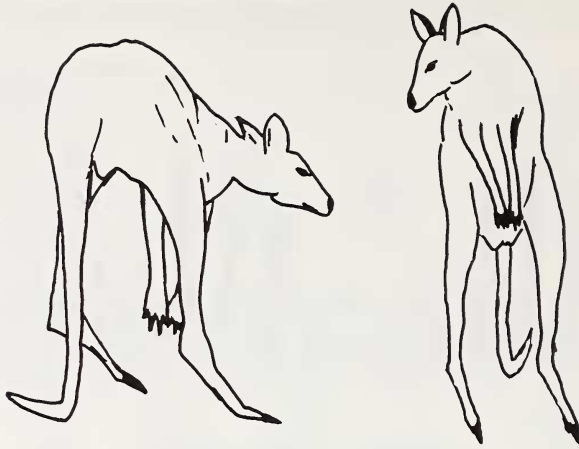
Fig. 2. Standing on tip-toes in broadside position during an agonistic encounter between two male agile wallabies

Ms was 'checked' by Mm; the younger male hissed and struck with his paws against the older before retreating.

Patterns of association

Females who were obviously approaching oestrus were persistently followed by 1–4 males. One large male (Ml) tended to follow the oestrous female continually whereas smaller males (Mm and/or Ms) remained within 20 m. Within these consort-groups sexual behaviour patterns resembled those of non-oestrous sexual interactions but male sexual behaviour was more frequent and vigorous. In 9 consort-groups females interacted with the consorting males at 2.82 interactions per hour (N = 8.5 hours of observation). Sexual behaviour of the smaller males was often interrupted by the approach of the largest and dominant male. No successful mounting and copulation was observed (N = 4 attempts). Data on duration and consistency of members within a consort-group were not collected because wallabies were too mobile to allow the collection of regular and continuous data.

The frequencies of associations for various size/sex classes performing foraging and resting behaviour are shown in table 3. In the monsoon forest the mean frequency of association were higher (foraging: 2.51, resting: 2.45 versus 2.21 and 1.62 respectively in the eucalypt woodland). Foraging and resting wallabies were more solitary in the eucalypt woodland than wallabies in the monsoon forest (19.6 and 30.4 % versus 10.7 % and 12.2 % respectively). Wallabies observed alone at the beginning of a 30 min observation bout remained so in 80 % of cases in the monsoon forest (N = 60 bouts) and in 86 % of bouts in the eucalypt woodland (N = 51) (Tab. 4).

Adult females with young-at-foot were recorded alone more frequently than other associations (Tab. 3). They occasionally associated with other wallabies when feeding but rarely did so when resting. Large and medium sized males were usually associated with mixed sex associations whereas small males were essentially solitary. Apart from the mother-young group, the most permanent association was between females in the eucalypt woodland. Four female pairs and one female trio were observed over 35–77 days (mean: 50.2 days). Most of these females were of different size-classes. Group members rested close together and were strongly cohesive when associated with other wallabies. Cohesive groups were most conspicuous during the late dry season when larger aggregations of wallabies were grazing and drinking at the billabong. Groups arrived and left this area with

Table 3. **Types of association and frequency (%) of each size/sex class in the late dry season**

Habitat	Activity	Association	Size/sex class						
			Ml	Mm	Ms	Fl	Fm	Fs	Fyaf
Eucalypt woodland	foraging	single	8.3	22.6	43.8	20.5	21.4	20.0	58.3
		N = 2 single sex	16.7	3.2	6.2	17.9	16.7	13.3	–
		N ≧ 3	8.3	3.2	6.2	7.7	9.5	13.3	16.7
		N = 2 mixed sex	0	22.6	12.5	5.1	14.3	6.7	–
		N ≧ 3	66.7	48.4	31.3	48.7	38.1	46.7	25.0
		No. indiv.	12	31	16	39	42	15	12 × 2
	resting	single	11.1	26.1	75.0	33.3	32.3	42.8	100
		N = 2 single sex	11.1	13.0	0	29.6	22.6	14.3	–
		N ≧ 3	0	0	0	3.7	6.4	0	0
		N = 2 mixed sex	33.3	43.5	12.5	22.2	22.6	14.3	–
		N ≧ 3	44.4	17.4	12.5	11.1	16.1	28.6	–
		No. indiv.	9	23	8	27	31	7	5 × 2
Monsoon forest	foraging	single	0	0	17.2	18.7	13.5	16.0	32.0
		N = 2 single sex	0	0	10.3	6.3	10.8	4.0	–
		N ≧ 3	0	14.3	10.3	16.7	16.2	16.0	28.0
		N = 2 mixed sex	0	9.5	20.7	6.3	10.8	4.0	–
		N ≧ 3	100	76.2	41.4	52.0	48.6	60.0	40.0
		No. indiv.	14	21	29	48	37	25	25 × 2
	resting	single	10.5	8.0	34.8	9.3	8.6	26.9	80.9
		N = 2 single sex	5.3	4.0	8.7	11.6	11.4	11.5	–
		N ≧ 3	0	0	0	7.0	17.1	15.4	0
		N = 2 mixed sex	5.3	8.0	4.3	7.0	2.9	0	–
		N ≧ 3	78.9	80.0	52.2	65.1	60.0	46.2	19.1
		No. indiv.	19	25	23	43	35	26	21 × 2

coordinated movements over the open grassy bed. Other individuals rarely joined in although some males temporary accompanied female groups. Next to the mother-young group, female pairs had the lowest lability index (Tab. 4). The mean change in composition per observation bout was 0.22 in monsoon forest (N = 31 bouts) and 0.08 in eucalypt woodland (N = 24).

In both habitats mixed sex associations (N ≥ 3 wallabies) were the most frequent type of association during foraging. These associations were not persistent through time as indicated by the highest lability indices (Tab. 4). The mean change in composition of mixed sex associations was 0.96 in monsoon forest (N = 22 bouts) and 1.31 in eucalypt woodland (N = 29).

Table 4. **Mean lability index of associations for foraging wallabies in two habitats**

Association	Monsoon forest			Eucalypt woodland		
	N_a	N_b	Index	N_a	N_b	Index
Single	23	60	0.2	35	51	0.14
Fyaf	8	22	0.07	7	25	0
N = 2 Single sex	6	31	0.11	10	24	0.04
N ≧ 3	7	22	0.15	3	8	0.16
N = 2 Mixed sex	8	28	0.1	9	21	0.11
N ≧ 3	18	54	0.23	17	29	0.25

N_a: No. of associations, N_b: No. of observation bouts.

Discussion

In the tropical lowlands of the Northern Territory of Australia, the agile wallaby *Macropus agilis*, occurs in various habitats with evident differences in population density. The widespread occurrence may be due to its general adaptability as a grazer and browser, and to its high fecundity compared with other tropical macropodids. Given its capability for continuous breeding (KIRKPATRICK and JOHNSON 1969; MERCHANT 1976) and the early sexual maturity of females at about 10–12 months of age (MERCHANT 1976), rapid population growth might be expected under favourable conditions. Despite the markedly seasonal climate, over 90 % of all adult females examined by BOLTON et al. (1982) were fully reproductive. At Kapalga, *M. agilis* is the most common macropodid in both habitats under study with low densities in the major habitat, the eucalypt woodland, and higher densities in the monsoon forest. The only other macropodid species present at the Kapalga area is the antilopine wallaroo *Macropus antilopinus*. This species is much less common in the open woodland and has never been observed at the monsoon forest site (CORBETT, pers. comm.). Monsoon forests are small restricted and isolated and are regarded as the most important fructivorous plant community of the Kakadu National Park region producing fleshy fruits and nectar all year round (TAYLOR and DUNLOP 1985). During the dry season the density of wallabies in the monsoon forest remained stable although free water was not available from the end of August until January. Wallabies in the monsoon forests were sedentary and presumably obtained their water requirements from fruits and roots. In contrast wallabies in the eucalypt woodland responded to seasonal availability of food and water by moving to permanent waters and associated green food supplies.

At both study sites adult females outnumbered males. This sex ratio has also been described for populations of other macropodids such as the whiptail wallaby, *Macropus parryi* (KAUFMANN 1974), the red kangaroo, *M. rufus* (NEWSOME 1977; JOHNSON and BAYLISS 1981), the eastern grey kangaroo, *M. giganteus* (JARMAN and SOUTHWELL 1986) and the western grey kangaroo, *M. fuliginosus* (NORBURY et al. 1988; ARNOLD et al. 1991) along with several explanatory hypotheses. JOHNSON and BAYLISS (1981) attributed the skewed ratio in a population of *M. rufus* to a higher mortality in males resulting possibly from dispersal into suboptimal habitats. NORBURY et al. (1988) argued that sexual dimorphism in body weight may impose higher nutritional demands for males which can be critically during periods of food shortage. A biased sex ratio might also result from different juvenile mortality in the sexes. RUSSELL (1982) showed that in marsupials heaviest mortality tend to fall after pouch life has been completed. In *M. rufogriseus*, for instance,

mortality was highest during the period when infants were still suckling from their mothers following them as young-at-foot (JOHNSON 1989a). The high mortality was attributed to the competition between females limiting their ability to sustain higher levels of lactation during late pouch life and early life out of pouch.

Reasons for the female-biased sex ratio of adult *M. agilis* are not obvious. Intrasexual competition in females may operate on a seasonal base, for example during the dry season when resources become limited and clumped, but also during the wet season in areas where dry season feeding grounds are flooded (cf. BOLTON et al. 1982). Furthermore, predation by dingoes, *Canis familiaris dingo*, may be a significant factor in juvenile mortality. At Kapalga, dingoes focus on seasonally available magpie geese, *Anseranas semipalmata* and dusky rats, *Rattus colletti*, but wallabies are the most consistent eaten prey throughout the year (CORBETT 1989) and predominate in those wet seasons when rat numbers are low (CORBETT pers. comm.). Solitariness of subadult male agiles suggests that sons separate earlier from their mothers than daughters of similar age. It is possible that by separation and dispersal into less suitable habitats, young males are exposed to greater dingo predation than young females.

Previous studies suggested that *M. agilis* is essentially solitary, its mean group size being close to unity (JOHNSON 1980; CROFT 1987). However, in JOHNSON's (1980) study more individuals were counted in association with other wallabies (N $\geq$ 478) than those seen alone (N = 395). Field studies conducted on different macropodid species analysed group size and composition which were regarded as an index of sociality and dispersion. Studies on *M. rufus* (NEWSOME 1965), eastern wallaroos, *M. r. robustus* (TAYLOR 1982), *M. giganteus* (TAYLOR 1982; SOUTHWELL 1984a) and *M. fuliginosus* (JOHNSON 1983) demonstrated a relationship between mean group size and population density, whereas JOHNSON (1989b) showed for *M. rufogriseus* that average group size varied seasonally, but was not influenced by population density. The different degree of gregariousness may therefore be a result of different population density rather than a truely social phenomenon especially when arbitrary defined distances between animals are used to denote a number of individually unknown animals as a group.

The results of this study indicate that the size of associations in *M. agilis* is also related to population density. During the dry and late dry season the mean size of associations was higher in the monsoon forest where wallaby density was greatest. Animals of different size/sex classes differed in the extent to which they were found alone or in association with other individuals. As in other macropodids, females with young-at-foot were the most solitary class (e.g. TAYLOR 1982; JARMAN and SOUTHWELL 1986). Small males were essentially solitary whereas large and medium sized males were always seen with a female or in larger mixed sex associations. This contrasts to macropodid species such as *M. rufus* and *M. giganteus* where large males were seen alone more often than other male classes (CROFT 1981b; JARMAN and SOUTHWELL 1986). This is believed to be due to their high mobility in search for oestrous females, and might therefore depend on the female breeding pattern. Males of the larger kangaroo species form transient rather than long-term consort-relationships with females approaching oestrus and a size-based dominance-hierarchy among males is regarded as determining final priority of access to oestrous females (RUSSELL 1984).

Larger associations in *M. agilis* lasted only for several hours and probably represented coincidental aggregations around a spatially concentrated resource such as water, fruiting trees, green grass, and shelter sites. Associations resembled those described for the gregarious macropodids with an unstable composition containing varying combinations of animals of all ages and both sexes (RUSSELL 1984; JARMAN and COULSON 1989). The duration of consort-groups, recognized by the high amount of sexual behaviour of males, could not be assessed because of the high mobility of these groups (cf. JARMAN and SOUTHWELL 1986). In the woodland a high proportion of female groups could be observed.

They were characterized not only by small distances between individuals but also by their persistence over time, by a cohesive and coordinated movement pattern and by the orientation of each member to the behaviour of other members. They might derive from mother-offspring units when daughters settle within their mothers' home range whilst sons disperse soon after weaning as described for *M. rufogriseus* (JOHNSON 1986). However, given the short duration of this study, it is not known how associations may change in the wet season and whether or not female groups are permanent social units. Moreover, factors that favour female group formation at low population density remain to be determined.

Acknowledgements

Zusammenfassung

Beobachtungen zum Verhalten und zur sozialen Organisation des Flink-Wallabys,
Macropus agilis (Gould, 1842), in zwei Habitaten Nordaustraliens

Es wurden Verhalten, Zusammensetzung und Stabilität der Verbände sowie Populationsmerkmale des Flink-Wallabys in zwei Habitaten Nordaustraliens – Monsunwald und Eukalyptussavanne – untersucht. Die Beobachtungen fanden über fünf Monate während der Trockenzeit im australischen Kapalga, Nord-Territorium, statt. Die Populationsdichte im Monsunwald war durchschnittlich 6,5 mal höher als die in der Eukalyptussavanne. In beiden Populationen war das Geschlechterverhältnis der Adulttiere signifikant in Richtung der Weibchen verschoben. Größere gemischtgeschlechtliche Verbände waren nicht dauerhaft und stellten Aggregationen an lokal begrenzten Ressourcen wie Wasserstellen, Weide- und schattigen Ruheplätzen dar. Ihre Größe korrelierte mit der Populationsdichte, die vom Habitat sowie der Verteilung und Verfügbarkeit der Nahrung abhängig zu sein scheint. Während mittelgroße und große Männchen überwiegend mit Weibchen verschiedener Größenklassen assoziiert waren, zeigten junge Männchen sowie Weibchen mit noch nicht entwöhntem Jungtier deutliche Tendenzen zu solitärer Lebensweise. Die beschriebenen sozialen Strukturen und Populationsmerkmale werden mit denen anderer bisher untersuchter Känguruharten verglichen. Die solitäre Lebensweise junger Männchen und die beobachteten stabilen Weibchen-Einheiten entstehen vermutlich durch den Verbleib weiblicher Nachkommen bei der Mutter, während die männlichen Nachkommen sich früh nach der Entwöhnung vom Muttertier trennen.

References

ALTMANN, J. (1974): Observational study of behavior: sampling methods. Behaviour **49**, 227–267.
ARNOLD, G. W.; GRASSIA, A.; STEVEN, D. E.; WEELDENBURG, J. R. (1991): Population ecology of western grey kangaroos in a remnant of wandoo woodland at Baker's Hill, southern Western Australia. Wildl. Res. **18**, 561–575.
BOLTON, B. L. (1974): An ecological study of the agile wallaby on the coastal plains of the Northern Territory with a comparison between improved and unimproved areas. MVSc thesis, Univ. Queensland, Brisbane.
BOLTON, B. L.; NEWSOME, A. E.; MERCHANT, J. C. (1982): Reproduction in the agile wallaby *Macropus agilis* (Gould) in the tropical lowlands of the Northern Territory: opportunism in a seasonal environment. Aust. J. Ecol. **7**, 261–277.
CORBETT, L. K. (1989): Assessing the diet of dingoes from feces: a comparison of 3 methods. J. Wildl. Manage. **53**, 2, 343–346.
CROFT, D. B. (1981a): Social behaviour of the euro, *Macropus robustus* (Gould), in the Australian arid zone. Aust. Wildl. Res. **8**, 13–49.
— (1981b): Behaviour of red kangaroos, *Macropus rufus* (Desmarest, 1822), in north-western New South Wales, Australia. Aust. Mammal. **4**, 5–58.
— (1987): Socio-Ecology of the antilopine wallaroo, *Macropus antilopinus*, in the Northern Terri-

tory, with observations on sympatric *M. robustus woodwardii* and *M. agilis*. Aust. Wildl. Res. **14**, 243–255.

GANSLOSSER, U. (1989): Agonistic behaviour in Macropodidoids – a review. In: Kangaroos, Wallabies and Rat-Kangaroos, Ed. by G. GRIGG, P. JARMAN, and I. HUME. Sydney: Surrey Beatty and Sons. Pp. 475–503.

JARMAN, P. J.; COULSON, G. (1989): Dynamics and adaptiveness of grouping in macropodids. In: Kangaroos, Wallabies and Rat-Kangaroos. Ed. by G. GRIGG, P. JARMAN, and I. HUME. Sydney: Surrey Beatty and Sons. Pp. 527–547.

JARMAN, P. J.; SOUTHWELL, C. J. (1986): Grouping, associations, and reproductive strategies in Eastern Grey Kangaroos. In: Ecological aspects of social evolution. Ed. by D. I. RUBENSTEIN and R. W. WRANGHAM. Princeton, USA: Princeton University Press. Pp. 399–428.

JOHNSON, C. N. (1983): Variation in group size and composition in red and western grey kangaroos, *Macropus rufus* (Desmarest) and *M. fuliginosus* (Desmarest). Aust. Wildl. Res. **10**, 25–31.

— (1986): Philopatry, reproductive success of females, and maternal investment in the red-necked wallaby. Behav. Ecol. Sociobiol. **19**, 143–150.

— (1989a): Mortality of immature red-necked wallabies. J. Mammalogy **70**, 202–204.

— (1989b): Grouping and the structure of association in the red-necked wallaby. J. Mammalogy **70**, 18–26.

JOHNSON, C. N.; BAYLISS, P. G. (1981): Habitat selection by sex, age and reproductive class in the Red Kangaroo, *Macropus rufus*, in Western New South Wales, Aust. Wildl. Res. **8**, 465–474.

JOHNSON, P. M. (1980): Field observations on group compositions in the agile wallaby *Macropus agilis* (Gould) (Marsupialia: Macropodidae). Aust. Wildl. Res. **7**, 327–331.

KAUFMANN, J. H. (1974): Social ethology of the whiptail wallaby, *Macropus parryi*, in north eastern New South Wales. Anim. Behav. **22**, 281–369.

KIRKPATRICK, T. H.; JOHNSON, P. M. (1969): Studies of Macropodidae in Queensland. 7. Age estimation and reproduction in the agile wallaby (*Wallabia agilis* (Gould)). Qd. J. Agric. Anim. Sci. **26**, 691–698.

McALPINE, J. R. (1976): Climate and water balance. In: Lands of the Alligator Rivers Area, Northern Territory. CSIRO Aust. Land Res. Ser. No. **38**, 35–49.

MERCHANT, J. C. (1976): Breeding biology of the agile wallaby *Macropus agilis* (Gould) (Marsupialia: Macropodidae) in captivity. Aust. Wildl. Res. **3**, 93–103.

— (1983): Agile Wallaby. In: Complete Book of the Australian Mammals. Ed. by R. STRAHAN. Sydney: Angus and Robertson. Pp. 242–243.

NEWSOME, A. E. (1965): The abundance of red kangaroos, *Megaleia rufa* (Desmarest), in central Australia. Aust. J. Zool. **13**, 269–287.

— (1977): Imbalance in the sex ratio and age structure of the Red kangaroo, *Macropus rufus*, in central Australia. In: The biology of marsupials. Ed. by B. STONEHOUSE and D. GILMORE. London: Macmillan Press. Pp. 221–233.

— (1983): The grazing Australian marsupials. In: Ecosystems of the World. 13: Tropical savannas. Ed. by F. BOURLIÉRE. Amsterdam: Elsevier. Pp. 441–461.

NIX, H. A. (1981): The environment of *Terra australis*. In: Ecological Biogeography of Australia. Ed. by A. KEAST. The Hague: W. Junk. Pp. 103–133.

NORBURY, G. L.; COULSON, G. M.; WALTERS, B. L. (1988): Aspects of the western grey kangaroo, *Macropus fuliginosus melanops*, in semi-arid north-west Victoria. Aust. Wildl. Res. **15**, 257–266.

RIDPATH, M. G. (1985): Ecology in the wet-dry tropics: how different? Proc. Ecol. Soc. Aust. **13**, 3–20.

RUSSELL, E. M. (1982): Patterns of parental care and parental investment in marsupials. Biol. Rev. **57**, 423–486.

— (1984): Social behaviour and social organisation of marsupials. Mammal. Rev. **14**, 3, 101–154.

SOUTHWELL, C. J. (1984a): Variability in grouping in the eastern grey kangaroo, *Macropus giganteus*. I. Group density and group size. Aust. Wildl. Res. **11**, 423–435.

— (1984b): Variability in grouping in the eastern grey kangaroo, *Macropus giganteus*. II. Dynamics of group formation. Aust. Wildl. Res. **11**, 437–449.

— (1989): Techniques for monitoring the abundance of kangaroo and wallaby populations. In: Kangaroos, Wallabies and Rat-Kangaroos. Ed. by G. GRIGG, P. JARMAN, and I. HUME. Sydney: Surrey Beatty and Sons. Pp. 659–693.

TAYLOR, R. J. (1982): Group size in the eastern grey kangaroo, *Macropus giganteus*, and the wallaroo, *Macropus robustus*. Aust. Wildl. Res. **9**, 229–237.

TAYLOR, J. A.; DUNLOP, C. R. (1985): Plant communities of the wet-dry tropics of Australia: the Alligator Rivers region, Northern Territory. Proc. Ecol. Soc. Aust. **13**, 83–127.

Author's address: Dipl.-Biol. WOLFGANG DRESSEN, Lehrstuhl für Verhaltensphysiologie, Fakultät für Biologie, Universität Bielefeld, Postfach 10 01 31, D-33501 Bielefeld, Germany